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Multivariate Analysis of Allozyme and Morphometric Variability in *Racosperma auriculiforme* and *R. mangium*

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Summary

We investigated the levels and distribution of genetic variation of *Racosperma auriculiforme* (*Acacia auriculiformis*) and *R. mangium* (*A. mangium*), using multivariate analysis of allozymes and phenotypic attributes. The patterns of genetic variation based on allozymes were similar to those based on phenotypic attributes for *R. auriculiforme*. In *R. mangium*, there was, however, a lack of correspondence between phenotypic attributes and allozymes. For *R. auriculiforme*, these results suggest that initial isozyme surveys of a limited number of populations covering the species'geographic range could help define more efficient sampling strategies for intense seed collections and large scale provenance-progeny tests. For *R. mangium*, the results, however, suggest that we should rely mainly on genecological studies to establish guidelines for seed transfer in applied tree improvement programs. The allozyme diversity revealed that *R. mangium* was genetically depauperate compared to *R. auriculiforme*. The genecological diversity in quantitative traits over four sites indicated that *R. auriculiforme* is more plastic than *R. mangium*, both showing a geographical pattern of population differentiation. Genetic diversity parameters were negatively correlated with the latitude for *R. auriculiforme*, suggesting Papua New Guinea as a centre of diversity. On the other hand, genetic diversity parameters were negatively correlated with the elevation for *R. mangium*. Canonical correlation analysis revealed two and one significant canonical variates for *R. auriculiforme* and *R. mangium*, respectively. It also revealed significant association between geographic origins and some allozymes and adaptive quantitative traits. Both principal components and discriminant analyses revealed a clear pattern of population grouping related to taxon delineation and could be used to detect possible introgression between the two species. For both species, factor and discriminant variable scores, derived from principal components and discriminant analyses, exhibited strong relation with location variables: latitude, longitude and elevation.

Key words: Acacia, genetic variation, plantation forestry in the tropics, multivariate analysis, *Racosperma*, social forestry.

Introduction

In most tropical countries, migratory slash-and-burn agriculture, along with modern agriculture, fuelwood gathering, selective logging, mining, and bush fires, all intimately linked to a rapid expansion in human population, are reported to be the main causes of loss of forest biodiversity and environment degradation (KHASA et al., 1995a; KHASA and DANCIK, 1997). In

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reaction to the rapid loss of tropical forests, urgent measures to promote reforestation and agroforestry should be undertaken to achieve a sustainable development. *Racosperma auriculiforme* (CUNN. ex BENTH.) PEDLEY (*Acacia auriculiformis*) and *R. mangium* (WILLD.) PEDLEY (*A. mangium*), two fast-growing multipurpose tree species belonging to the *Leguminosae* family (*Mimosoideae* subfamily), are often given the highest priority for planting in the humid and subhumid tropics (KHASA et al., 1994a, 1995b).

R. auriculiforme and *R. mangium* are indigenous to Australia, Papua New Guinea, and Indonesia. *R. auriculiforme* grows in a variety of climatic and soil conditions from sea level to approximately 1,000 m in elevation (BOLAND et al., 1990; KHASA et al., 1994a). However, *R. mangium* is a stenohaline species which commonly occupies more restricted range of habitats (KHASA et al., 1994a). Since both species have a wide natural distribution, their populations are expected to exhibit a high level of variability for both morphometric and biochemical or molecular traits. The two species are mainly outcrossers (MORAN et al., 1989a, b; KHASA et al., 1993). They are closely related to each other (KHASA et al., 1994b) and there appears to be no major fertility barriers to interspecific hybridisation (SEDGLEY et al., 1992).

Due to the very recent domestication of these species, there are only a few reports of the patterns of natural genetic variation in both species (MORAN et al., 1989a, b; PINYOPUSARERK et al., 1991; WICKNESWARI and NORWATI, 1993; KHASA et al., 1994b, 1995c). These earlier studies, however, have used either allozyme or quantitative data but not both. In this study, we considered allozymes, quantitative traits and geographic locations simultaneously, and used several multivariate analyses to depict the population differentiation of both *Racosperma* species. Multivariate analysis provides statistical methods for study of the joint relationships of variables in data that contain intercorrelations (JAMES and MCCULLOCH, 1990).

Material and Methods

1. Plant material

Bulked seeds of *Racosperma* populations were sampled from natural stands and plantations and stored at 4 °C at low humidity (KHASA et al., 1994b). In this study, twenty five populations were analyzed for both allozyme and genecological diversities. Details on the geographical locations of the populations are provided in *table 1*. These populations were introduced into the Democratic Republic of the Congo (formerly Zaire) in common garden trials aimed at selecting the best productive provenances for fuelwood plantations and agroforestry. Seeds were germinated following prescribed pretreatments outlined by KHASA et al. (1994b, 1995c) for allozyme and genecological diversity analyses.

2. Allozyme diversity

The level and distribution of genetic diversity were evaluated within and among populations of each species, using starch gel electrophoresis (KHASA et al., 1994b). Enzyme loci where a comparison was possible between the two closely related species were used in this study. These loci were encoded by the following enzyme systems: aspartate aminotransferase (AAT, EC 2.6.1.1), glucose-6-phosphate dehydrogenase (G6P-DH, EC 1.1.1.49), leucine aminopeptidase (LAP, EC 3.4.11.1), malic enzyme (ME, EC 1.1.1.40), 6-phosphogluconate dehydrogenase (6-PGDH, EC 1.1.1.44), phosphoglucose isomerase (PGI,

Table 1. – Descriptions of the *Racosperma* seed sources and their origins.

	Geographical locations				
Species/Seedlot number	Locality[a]	Latitude (S) (deg. min.)	Longitude (E) (deg. min.)	Elevation (m)	Supplier[a]
R. auriculiforme					
A1. 15697	South of Coen Cape York, QLD	14°07'	143°16'	160	CSIRO
A2. 15985	Mount Molloy Rifle, CKQLD	16°41'	145°17'	380	id.
A3. 16107	Old Tonda Village, PNG	8°55'	141°33'	40	id.
A4. 16145	Wenlock River, QLD	13°06'	142°56'	130	id.
A5. 16149	Douglas River, NT	13°51'	131°09'	70	id.
A6. 16153	Cooper Creek, NT	12°06'	133°11'	40	id.
A7. 16159	Gerowie Creek, NT	13°29'	132°15'	100	id.
A8 16163	Elizabeth River, NT	12°36'	131°04'	40	id.
A9. 16355	Bensbach W Province, PNG	8°55'	141°15'	20	id.
A10. 3419n	Loudima, PN	4°35'	13°05'	166	CIRAD-F
A11. 3422n	Loudima, PN	4°11'	13°05'	166	id.
A12. Akzno	Kinzono, PB	4°35'	16°36'	650	CFK-SNR
R. mangium					
M1. 13459	Loudima, PN	4°11'	13°05'	166	CIRAD-F
M2. 13460	Loudima, PN	4°11'	13°05'	166	id.
M3. 13621	Piru, Ceram, IND	3°04'	128°12'	150	CSIRO
M4. 15367	7 km SSE of Mossman, QLD	16°31'	145°24'	60	id.
M5. 15635	Bloomfield, QLD	15°58	145°21'	100	id.
M6. 15643	Wemenever, PNG	8°43'	141°29'	40	id.
M7. 15644	Oriomo, PNG	8°50'	143°08'	10	id.
M8. 15677	Iron Range, QLD	12°43'	143°14'	40	id.
M9. 15687	South east of Daintree, QLD	16°16'	145°22'	12	id.
M10. 15690	Murray R. Cardwell, QLD	18°04'	145°53'	20	id.
M11. 15693	Lannercost South of Ingha, QLD	18°37'	145°54'	170	id.
M12. 15694	66 km North of Townsville, QLD	18°57'	146°17'	20	id.
M13. Mkzno	Kinzono, PB	4°35'	16°36'	650	CFK-SNR

[a]) Abbreviations: CFK-SNR: Centre forestier de kinzono-service national de reboisement (Democratic Republic of Congo, DRC); CSIRO: Commonwealth Scientific and Industrial Research Organisation (Australia); CIRAD: Centre de coopération internationale en recherche agronomique pour le développement; IND: Indonesia; NT: Northern Territory; PB: Plateau de Bateke (DRC); PN: Pointe-Noire (Congo); PNG: Papua-New Guinea; QLD: Queensland.

EC 5.3.1.9), and phosphoglucomutase (PGM, EC 5.4.2.2). Allozyme diversity was assessed with the Biosys-1 computer program (SWOFFORD and SELANDER, 1989), using standard measures: percent polymorphic loci (P), mean number of alleles per locus (A), and gene diversity (H_e, or expected heterozygosity).

3. Genecological diversity

We examined the distribution of genetic variation in juvenile growth, adaptative and morphological traits (quantitative traits) for 12 populations of *R. auriculiforme* and 13 populations of *R. mangium* by establishing a randomized complete block provenance trial on four sites in the Democratic Republic of the Congo. Measurements of these quantitative traits were taken at different ages in the nursery and field. Variables measured at 21 months in the field have been shown to be useful in explaining patterns of variation (KHASA et al., 1995c). These variables were: volume, survival rate, wood specific gravity, number of stems, and stem straightness. Rooting ability index of cuttings was also assessed (KHASA et al., 1995d).

4. Analysis of data

Allozyme diversity parameters at the population level (P, A, H_e) were correlated with population averages for growth, morphological traits, survival, and location variables using the SAS CORR procedure (SAS Institute Inc., 1989). Location variables of exotic stands were not included in the analyses. Normality and homoscedasticity of phenotypic distributions were tested using the SAS UNIVARIATE procedure and transformations were applied where necessary (KHASA et al., 1995c). Allozyme profiles of individuals were translated into coded vectors according to their multilocus genotypes (SMOUSE and WILLIAMS, 1982; YEH et al., 1985; CHELIAK et al., 1988; BOUSQUET et al., 1990). In this algorithm, each polymorphic locus was transformed into a vector of n-1 independent dimensions, where n is the number of alleles at a particular locus (SMOUSE and WILLIAMS, 1982). For example, the three genotypes (11, 12, 22) of a locus with two alleles (1 and 2) were translated into a vector Y' = [1, 1/2, 0]. The vector Y'= [1 0, 1/2 1/2, 1/2 0, 0 1, 0 1/2, 0 0] represented 6 genotypes 11, 12, 13, 22, 23, and 33, respectively, at a triallelic locus (1, 2, and 3). These multilocus coded profiles were then subjected to canonical correlation (CCA), canonical discriminant (CDA), and principal components (PCA) analyses using the SAS CANCORR, CANDISC and FACTOR procedures, respectively (HAIR et al., 1998). Thirteen polymorphic loci (*Aat-1, Aat-2, Aat-3, G6-pdh, Lap-1, Lap-2, Me-1, Me-2, 6-Pgdh-2, Pgi-1, Pgi-2, Pgm-1,* and *Pgm-2*) and quantitative traits were used in these analyses.

Population centroids were plotted on the first two axes or functions, the scale being made proportional to the eigenvalue. The individual scores obtained on the two first axes or functions were separately submitted to a one-way analysis of variance (see BOUSQUET et al., 1990) to quantify the proportion of total variance explained by a population effect on each of the two first axes or functions. A posteriori multiple comparison of population means was conducted, using the BONFERRONI's correction for multiple pairwise comparisons with a maximum experimentwise error rate of 5%. Factorial or discriminant scores for the first two principal components or discriminant functions were fitted to location variables by multiple regression using the REG procedure. Since patterns for both allozymes and quantitative traits are usually non-linear, we used a second-order trend surface model of the geographic variables (WESTFALL and CONKLE, 1992). The preliminary model included quadratic and interaction terms in addition to linear terms for all geographic variables. From the preliminary model, a final equation was selected by backward elimination method.

Results

Estimates of allozyme, growth, morphological and adaptative variability of the different populations of *R. auriculiforme* and *R. mangium* are given in *table 2*. Mean numbers of alleles per locus within populations (A_p) were 1.9 and 1.5 for *R. auriculiforme* and *R. mangium*, respectively. The mean percentage of polymorphic loci within populations (P_p) was 51% (0.99 criterion) for *R. auriculiforme* and 24% (0.99 criterion) for *R. mangium*. Gene diversity (H_{ep}, or expected heterozygosity) was 0.114 for *R. auriculiforme* and 0.064 for *R. mangium*. Mean heterozygosity was moderate for *R. auriculiforme* and low for *R. mangium* relative to other cultivated tropical taxa (LOVELESS, 1992). The mean genetic diversity measures (A_p, P_p, and H_{ep}) were negatively correlated with the latitude for *R. auriculiforme* (*Table 3*), suggesting populations from lower latitudes such as those from Papua New Guinea were more diverse on average than populations from higher latitudes in Australia. With one exception in Queensland, we found that H_{ep} was highest in *R. auriculiforme* populations from Papua-New Guinea (PNG) and lowest in populations from the Northern Territory (NT) and Queensland (QLD) (*Tables 1* and *2*). This trend, however, was not observed for *R. mangium*. For this species, populations from QLD had higher but not significantly different H_{ep} values (at $P < 0.05$, using a paired STUDENT's t-test) than those from PNG and genetic diversity parameters were negatively correlated with the elevation.

For *R. auriculiforme*, volume and stem straightness were negatively correlated with latitude, suggesting that populations from lower latitude (e.g. PNG with the highest H_{ep}) are most productive and straighter in tropical regime climates such as observed in the Democratic Republic of the Congo. The number of stems per tree was negatively correlated with rooting ability index of cuttings, longitude, and altitude, and positively correlated with survival, and stem straightness, which in turn was negatively correlated with all geographic variables (*Table 3*). For *R. mangium*, negative correlations were found between number of stems and heterozygosity parameters (Ap and Pp) while positive correlations were observed between stem straightness, wood specific gravity and number of stems. In addition, volume was positively correlated with survival and negatively correlated with stem straightness, wood specific gravity, number of stems, elevation, and rooting ability index of cuttings was positively correlated with latitude and longitude (*Table 3*). *R. auriculiforme* had relatively high survival rate, wood specific gravity, number of stems per tree, and heterozygosity parameters, while it had low volume, rooting ability index and stem straightness as compared to *R. mangium* (*Table 2*).

Using three criteria (HAIR et al., 1998): (1) the level of statistical significance of the function, (2) the eigenvalues, and (3) the canonical redundancy analysis, only the two first canonical functions of the canonical correlation analysis could be interpreted for *R. auriculiforme* and the first one for *R. mangium*. For *R. auriculiforme*, the coded variable *Pgi-2b* (with a standardized canonical coefficient of 0.87, correlation of 0.92) on the first canonical variate (47% of the total variation) accounted for a major portion of the correlation between allozymes and quantitative traits (VOL, correlation of 0.36), and geographic origin (LONG, correlation of 0.72; ELV, correlation of 0.31) and *Pgm-1b* (with a standardized canonical coefficient of 0.86, correlation of 0.79) on the second canonical variate (20% of the total variation) accounted for a major portion of the correlation between allozymes and quantitative traits (VOL, correlation of 0.43; SV, correlation of 0.30; RAIC, correlation of –0.68; WSG, correlation of –0.3; NS, correlation of 0.74; ST, correlation of

Table 2. – Estimates of allozyme, growth, morphological and adaptative variability of various populations of *R. auriculiforme* and *R. mangium*[a]).

Species/pop.#	A_p	P_p (0.99)	H_{ep}	VOL	SV	WSG	NS	ST	RAIC
R.auriculiforme									
A1	1.4 (0.1)	27.8	0.068 (0.031)	1 287.9 ab	87.1 a	0.52 ab	1.2 e	0.4 d	1.16 a
A2	1.6 (0.2)	38.9	0.080 (0.031)	802.1 b	88.9 a	0.51 ab	1.4 de	0.5 cd	0.06 bc
A3	2.4 (0.2)	77.8	0.125 (0.027)	1 524.5 a	91.6 a	0.52 ab	1.8 abc	0.9 a	---
A4	2.4 (0.2)	83.3	0.177 (0.039)	765.3 c	83.0 ab	0.50 ab	1.3 e	0.5 cd	0.21 bc
A5	1.9 (0.2)	44.4	0.100 (0.038)	1 392.9 a	89.7 a	0.49 b	2.0 ab	0.7 abc	-0.25c
A6	1.6 (0.2)	38.9	0.075 (0.030)	993.0 ab	91.6 a	0.52 ab	2.0 ab	0.8 ab	0.36 bc
A7	2.1 (0.2)	61.1	0.129 (0.040)	770.2 c	93.3 a	0.50 ab	1.8 abc	0.9 a	0.20 bc
A8	2.0 (0.2)	55.6	0.118 (0.037)	953.4 b	94.3 a	0.54 a	1.6 cde	0.7 abc	0.61 ab
A9	2.4 (0.1)	72.2	0.183 (0.041)	1 564.9 a	93.0 a	0.52 ab	1.7 bcd	0.8 ab	-0.34 c
A10	1.4 (0.2)	33.3	0.110 (0.048)	1 292.4 ab	84.1 ab	0.53 ab	1.7 bcd	0.8 ab	0.65 ab
A11	1.6 (0.2)	38.9	0.115 (0.050)	1 402.4 a	79.6 b	0.53 ab	2.1 a	0.9 a	-0.22 c
A12	1.7 (0.2)	33.3	0.086 (0.040)	925.7 b	88.5 a	---	1.8 abc	0.8 ab	-0.04bc
Mean	1.9	50.5	0.114	1 139.5	88.7	0.52	1.7	0.7	0.22
	(0.1)	(5.5)	(0.011)	(87.0)	(1.3)	(0.004)	(0.08)	(0.05)	(0.13)
Species/pop.#	A_p	P_p (0.99)	H_{ep}	VOL	SV	WSG	NS	ST	RAIC
R. mangium									
M1	1.8 (0.2)	33.3	0.059 (0.035)	8 770.8 a	51.2 de	0.44 b	1.2 a	0.2 de	---
M2	1.4 (0.2)	22.2	0.043 (0.034)	8 735.1 a	70.2 abc	0.46 b	1.3 a	0.3 cde	0.73 ab
M3	1.3 (0.2)	22.2	0.049 (0.033)	703.8 d	47.2 e	---	1.3 a	0.7 a	-0.42 c
M4	1.5 (0.2)	16.7	0.042 (0.032)	607.8 d	61.4 bcde	0.44 b	1.3 a	0.4 bcd	0.26 bc
M5	1.3 (0.2)	16.7	0.055 (0.038)	2 483.5 bcd	61.6 bcde	0.45 b	1.2 a	0.1 e	1.46 a
M6	1.3 (0.1)	22.2	0.046 (0.035)	2 707.7 bcd	78.3 ab	0.46 b	1.3 a	0.4 bcd	0.49 bc
M7	1.7 (0.2)	33.3	0.069 (0.036)	3 591.4 bc	87.5 a	0.44 b	1.1 a	0.2 de	0.90 ab
M8	1.3 (0.1)	22.2	0.074 (0.040)	3911.3 b	78.1 ab	0.45 b	1.3 a	0.3 cde	0.77 b
M9	1.7 (0.2)	33.3	0.103 (0.043)	2 165.5 bcd	59.4 bcde	0.44 b	1.2 a	0.3 cde	1.63 a
M10	1.6 (0.2)	27.8	0.100 (0.047)	1 217.9 cd	77.3 ab	0.48 ab	1.3 a	0.5 abc	1.32 ab
M11	1.4 (0.2)	22.2	0.058 (0.034)	778.8 d	66.9 abcde	0.56 a	1.3 a	0.6 ab	1.29 ab
M12	1.1 (0.1)	5.6	0.035 (0.035)	574.4 d	74.9 abc	---	1.4 a	0.4 bcd	1.45 ab
M13	1.6 (0.2)	38.9	0.098 (0.036)	1 584.4 bcd	52.2 de	0.44 b	1.2 a	0.5 bcd	1.36 ab
Mean	1.5	24.3	0.064	2 910.2	66.6	0.46	1.3	0.4	0.94
	(0.06)	(2.5)	(0.006)	(781.8)	(3.4)	(0.01)	(0.02)	(0.05)	(0.17)

[a]) Abbreviations: A_p = mean number of alleles per locus; P_p = percentage of polymorphic loci (0.99 criterion, a locus is considered polymorphic if the frequency of the most common allele is 0.99 or less); H_{ep} = HARDY-WEINBERG expected heterozygosity; VOL = volume (cm^3/tree); SV= survival (%); WSG = Wood specific gravity (g/cm^3); NS = number of stems/tree; ST= stem straightness (0 = straight, 1 = average, 2 = crooked); RAIC = rooting ability index of cuttings. Numbers in parentheses indicate the standard errors. Details of methods for estimating allozyme and genecological diversities are presented in (KHASA et al., 1995b,c) and in (KHASA et al., 1995d) for quantifying rooting ability index of cuttings. Note: Means followed by the same letter for each species are not significantly different using the BONFERRONI's multiple pairwise comparisons with a maximum experimentwise error rate of 5%.

0.76). Canonical correlation analysis for *R. mangium* revealed that 32% of the variation in allozyme variables was accounted for by the geographic variables. The coded variables *6-Pgdh-2a* (correlation of 0.37) and *6-Pgdh-2b* (correlation of –0.37) accounted for a major portion of the correlation between allozymes and the geographic origin (LAT, correlation of –0.51; LONG, correlation of -0.31). The percent of variation described by the first i canonical vectors was derived by $R^2 = \Sigma E_i/(1+\Sigma E_i)$, where E_i is the i'th eigenvalue (see WESTFALL and CONKLE, 1992).

The first axis of both principal components and discriminant analyses showed a clear pattern of population grouping related to taxon delineation (see *Fig. 1A*). The two first principal components (PCs) accounted for 27% of the total variance observed in the data set for both *Racosperma* species, with the first principal component contributing most of the variance (20%). The biological meaning of the major axis as determined by examining the eigenvectors (weights) and correlations of original variables with PC scores (loadings) (IEZZONI and PRITTS, 1991; HAIR et al., 1998) was dominated by variables *Aat-3b, Aat-3c, Pgi-2b, Me-1a, Me-1b,* SV, RAIC, WSG, NS, and ST (*Table 4*). This axis was mainly responsible for a clear pattern of population grouping related to taxon delineation (*Table 5, Fig. 1A*). The second axis, dominated by large component loadings from the variables *6-Pgdh-2a* and *6-Pgdh-2b*, was responsible for the isolation of populations M9 and M13 from the remaining populations of *R. mangium* (*Tables 4* and *5, Fig. 1A*). Populations A1 and A4 were the most completely differentiated from the remaining populations for *R. auriculiforme*. The first canonical discriminant function (CDF) was dominated by large contribu-

Table 3. – PEARSON product-moment correlation matrix: coefficients among genetic and genecological diversity parameters and the geographic origin of the populations for *R. auriculiforme* (above diagonal, df = 10) and *R. mangium* (below diagonal, df =11)[a]).

	Ap	Pp	Hep	VOL	SV	WSG	NS	ST	RAIC	LAT	LON	ELV
Ap	--------	0.978** *	0.917** *	0.211	0.091	-0.094	0.166	0.494	-0.575*	-0.675**	0.036	-0.475
Pp	0.863** *	--------	0.903** *	0.085	-0.026	-0.070	0.049	0.409	-0.469	-0.625*	0.138	-0.392
Hep	0.723**	0.772**	--------	0.102	-0.038	-0.105	-0.042	0.269	-0.503*	-0.553*	0.129	-0.382
VOL	0.221	0.464	0.321	--------	0.234	0.142	0.285	0.264	-0.219	-0.656*	0.104	-0.477
SV	0.132	0.145	0.136	0.546*	--------	0.460	0.621*	0.757**	-0.175	-0.394	-0.575*	-0.437
WSG	-0.220	-0.134	-0.077	-0.500	-0.061	--------	-0.152	0.061	0.490	-0.349	0.014	-0.236
NS	-0.706**	-0.725**	-0.414	-0.598*	-0.150	0.418	--------	0.828** *	-0.525*	-0.384	-0.711**	-0.567*
ST	-0.181	-0.084	-0.143	-0.680**	-0.389	0.744**	0.580*	--------	-0.480	-0.647*	-0.533*	-0.640*
RAIC	0.173	0.036	0.441	0.119	0.332	0.264	-0.144	-0.479	--------	0.277	0.096	0.087
LAT	0.032	-0.295	0.187	-0.307	0.140	0.470	0.264	-0.190	0.778** *	--------	0.034	0.792**
LON	0.2006	-0.091	0.229	0.105	0.496	0.354	-0.041	-0.520*	0.810** *	0.873** *	--------	0.555*
ELV	-0.599*	-0.556*	-0.550*	-0.567*	-0.604*	0.779**	0.390	0.556*	-0.290	-0.091	-0.411	--------

[a]) See *table 2* for definition of abbreviations.
* = 0.1 > (P% = 0) > 0.05; ** = 0.05 > (P% = 0) > 0.01; *** = (P% = 0) < 0.01

Table 4. – Loadings of varimax rotated principal components and canonical discriminant analyses for *R. auriculiforme* and *R. mangium*[a]).

Variables[b]	Coded variable	F1	F2	CAN1	CAN2
Aat-3	a	-0.077	0.008	0.080	-0.094
	b	-0.921***	-0.020	0.971***	0.050
	c	0.933***	0.016	-0.976***	-0.042
Pgi2	a	-0.098	-0.027	0.093	-0.059
	b	-0.526*	-0.011	0.506*	-0.012
Pgm-1	a	0.187	0.022	-0.288	-0.031
	b	-0.295	-0.029	0.428*	-0.074
6-Pgdh-2	a	-0.067	-0.978***	0.106	-0.072
	b	0.057	0.979***	-0.094	0.074
Me-1	a	-0.921***	-0.022	0.982***	0.033
	b	0.926***	0.019	-0.978***	-0.028
VOL	----	-0.201	-0.071	0.302	-0.492*
SV	----	0.479*	0.032	-0.431*	-0.243
RAIC	----	-0.726**	-0.069	0.665**	0.397*
WSG	----	0.570**	0.089	-0.622**	0.748**
NS	----	0.843***	-0.000	-0.777**	-0.186
ST	----	0.753**	0.019	-0.670**	0.142
Eigenvalue		7.33 (20%)	2.49 (7%)	120.79 (76%)	13.17(8%)
Cumulative % of total variance explained		20%	27%	76%	84%

[a]) ***, **, *: Very significant, significant and moderately significant loadings, with 60% or more of variance included in that principal component or function, between 30 and 60% of variance, and between 15 and 30% of variance, respectively.
[b]) Only variables with significant loadings are shown; see *table 2* for definition of variables.

tions from variables *Aat-3b, Aat-3c, Pgi-2b, Pgm-1b, Me-1a, Me-1b,* VOL, SV, RAIC, WSG, NS, and ST (*Table 4*). As for PCA, this function was mainly responsible for a clear pattern of population grouping related to taxon delineation (*Table 5, Fig. 1B*). The second CDF was dominated by large contributions from variables VOL, RAIC, and WSG (*Table 4*). Cross-validation using the analysis sample (50% of the total sample) and validation sample (50% of the total sample) with PROC DISCRIM indicated that the percentage of population classification was extremely high (>90%). Overall, both multivariate techniques provided almost the same patterns of population differentiation, although the total of variation explained by the

Table 5. – Analysis of variance on individual factorial or canonical scores obtained on the first two axes, based on transformed multilocus allozyme and morphometric data for 25 populations of *R. auriculiforme* (AUR) and *R. mangium* (MAN)[a].

Species/pop.	F1	F2	CAN1	CAN2
R. auriculiforme				
A3	1.45 A	-0.08 AB	-12.57 HI	-0.07 FG
A6	1.46 A	-0.39 AB	-15.55 M	-1.31 HIJ
A5	1.45 A	0.11 AB	-15.00 LM	-5.65 O
A13	1.34 AB	0.04 AB	-13.89 JK	0.38 EF
A7	1.30 ABC	0.11 AB	-14.15 KL	-1.95 IJKL
A11	1.21 BC	0.07 AB	-13.31 IJK	1.38 D
A10	1.13 CD	0.18 A	-12.57 HI	1.09 DE
A12	1.09 CDE	0.09 AB	-13.08 HIJ	1.08 DE
A2	0.93 DE	0.09 AB	-11.06 G	-0.32 FG
A9	0.90 E	0.11 AB	-12.27 H	3.61 C
A1	0.34 F	-0.00 AB	-9.10 F	3.45 C
A4	0.11 G	-0.05 AB	-9.50 F	-0.88 GH
Average	1.06 ± 0.13	0.02 ± 0.04	-12.67 ± 0.57	0.07 ± 0.72
R. mangium				
M11	-0.56 H	0.23 A	7.77 CD	7.13 B
M4	-0.56 H	0.23 A	7.09 DE	-3.98 N
M3	-0.65 HI	0.18 A	8.31 BC	-2.14 JKL
M1	-0.71 HIJ	0.31 A	10.16 A	-2.07 IJKL
M7	-0.76 HIJ	0.28 A	9.13 B	-2.74 LM
M5	-0.77 HIJ	0.26 A	8.35 BC	-3.28 MN
M6	-0.77 HIJ	0.30 A	9.09 B	-2.45 LM
M12	-0.79 IJ	0.18 A	6.89 E	8.67 A
M9	-0.84 IJ	-1.70 C	10.20 A	-1.51 HIJK
M2	-0.86 IJ	-0.02 AB	10.71 A	-2.18 KL
M10	-0.87 IJ	0.22 A	10.07 A	0.83 DE
M8	-0.88 JK	0.26 A	10.00 A	-2.50 LM
M13	-1.09 K	-0.60 B	10.53 A	-1.30 HI
Average	-0.78 ± 0.04	0.01 ± 0.16	9.10 ± 0.36	-0.58 ± 1.09
Population effect	93%**	23%**	99%**	93%**

[a]) Means followed by the same letter within a column are not significantly different at 5% significance level, using BONFERRONI (Dunn) t-test. Note: * and ** indicate level of significance at $P = 0.05$ and 0.01, respectively.

Table 6. – Quadratic regression analysis of canonical scores CAN1 and CAN2 (Backward elimination procedure[1]).

	R. auriculiforme				*R. mangium*			
Canonical Variable	Independent variables	Parameter Estimate	Prob. > F	Type III Sum of Squares	Independent variables	Parameter Estimate	Prob. > F	Type II Sum of Squares
CAN1	Intercept	59642.38	0.0001	8271.10	Intercept	21708.42	0.0001	219.726
	ELV	8.613	0.0001	1003.52	ELV	0.010	0.0001	74.276
	LONG	-800.952	0.0001	8132.13	LONG	-444.52	0.0001	257.938
	LAT	-796.414	0.0001	6115.06	LAT	1148.789	0.0001	367.198
	$LONG^2$	2.700	0.0001	7986.34	$LONG^2$	2.065	0.0001	281.429
	LAT^2	3.069	0.0001	1589.93	LAT^2	3.174	0.0001	429.977
	ELV^2	0.000	0.0001	96.61	ELV^2	0.002	0.0001	500.876
	LONG X ELV	-0.064	0.0001	941.99	LONG X ELV	0.074	0.0001	371.429
	LONG X LAT	5.156	0.0001	6307.89	LONG X LAT	-8.564	0.0001	370.037
					LAT X ELV	-0.691	0.0001	389.076
			R-square =	0.999			R-square =	0.947
CAN2	Intercept	-13397.26	0.0001	417.336	Intercept	23654.38	0.0001	260.884
	ELV	-4.860	0.0001	319.460	ELV	-0.0089	0.0001	50.607
	LONG	195.270	0.0001	483.353	LONG	-500.816	0.0001	327.411
	LAT	54.563	0.0001	28.703	LAT	1367.24	0.0001	520.129
	$LONG^2$	-0.704	0.0001	542.675	$LONG^2$	2.365	0.0001	369.083
	LAT^2	0.774	0.0001	101.209	LAT^2	3.397	0.0001	492.470
	ELV^2	-0.001	0.0001	212.536	ELV^2	0.003	0.0001	1805.03
	LONG X ELV	0.0371	0.0001	315.564	LONG X ELV	0.0916	0.0001	563.005
	LONG X LAT	-0.552	0.0001	72.402	LONG X LAT	-10.131	0.0001	517.872
					LAT X ELV	-0.857	0.0001	598.886
			R-square =	0.997			R-square =	0.911

[1]) All variables left in the models are significant at the 0.1000 level.

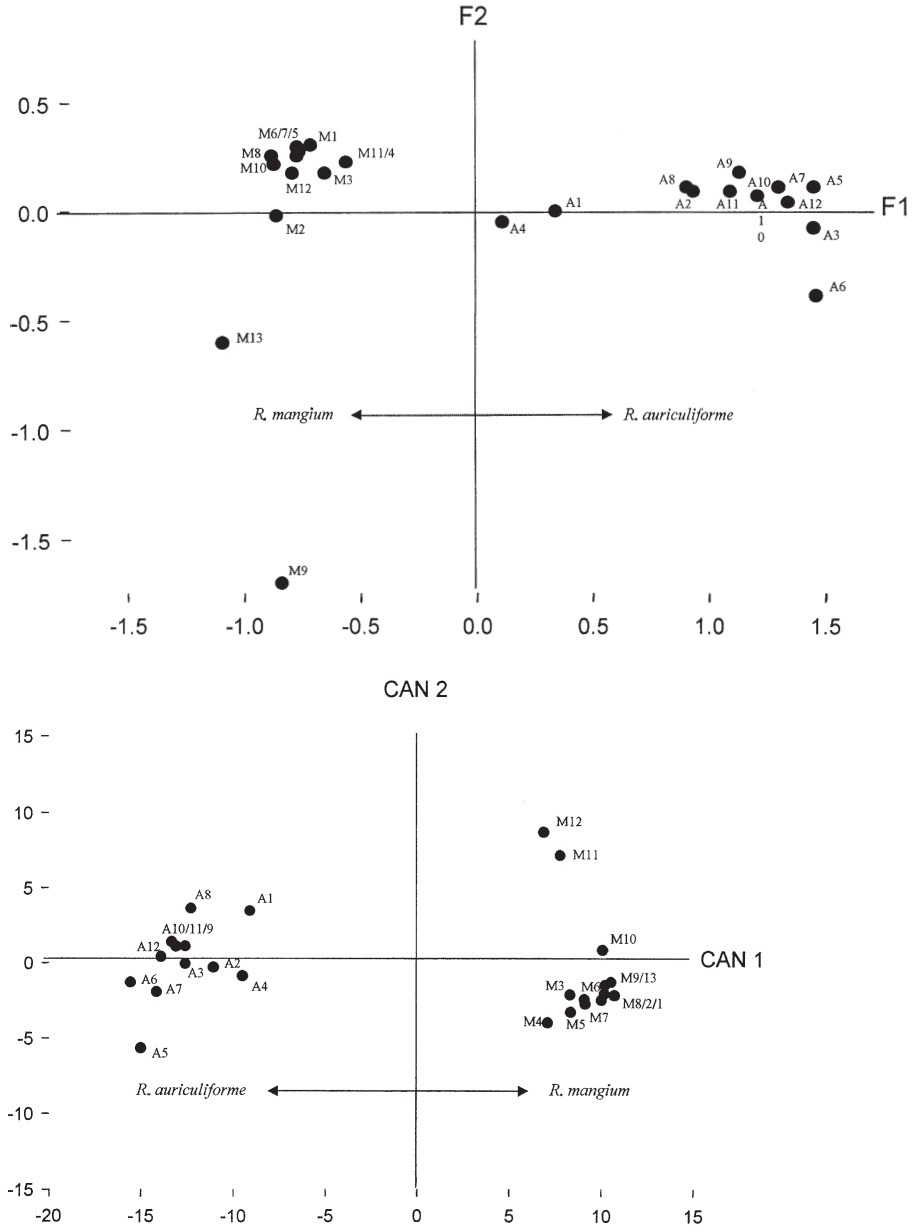

Fig. 1. – Plot showingh the centroids of provenances of *R. auriculiforme* and *R. mangium* on the first two PC axes (F1, F2) (A) or on the first two DF axes (Can1, Can2) (B).

first two CDFs was mathematically larger than that explained by the two first PCs due to the different estimation procedures (*Tables 4* and *5*).

Analysis of variance of the individual scores on the two first PCs, accounting for 20% and 7% of the total variance, respectively, showed that the population effect was highly significant on the first PC with 94% of the total variance (*Table 5*). The multiple comparisons of population means revealed 14 groups significantly different on the first PC and 3 groups on the second PC ($P < 0.05$). The discriminatory power was increased using CDA, with 17 groups significantly different on the first CDF and 15 groups on the second CDF. For *R. auriculiforme*, the calculated centroid (mean) values were 1.06 ± 0.13 and 0.02 ± 0.04 on the first two PCs, and –12.67 ± 0.57 and 0.07 ± 0.72 on the first two CDFs. The calculated centroid values were –0.78 ± 0.04 and 0.01 ± 0.16 on the first two PCs, and 9.10 ± 0.36 and –0.58 ± 1.09 on the first two CDFs for *R. mangium*. Regression of discriminant scores on geographic variables accounted for 99.9% of the variation for CAN1-scores and 99.7% for CAN2-scores, for *R. auriculiforme*; and 94.7% for CAN1-scores and 91.1% for CAN2-scores, for *R. mangium* (*Table 6*). Similarly, regression of factor scores on geographic variables accounted for 95.1% of the variation for PC1-scores and 17% for PC2-scores, for *R. auriculiforme*; and 88.2% for PC1-scores and 26.6% for PC2-scores, for *R. mangium* (results not shown). The final models shown in *table 6* retained only terms significant at $P < 0.1000$ level.

Discussion

Several factors, including tree size, longevity, fecundity, breeding system and geographic distribution, can influence the patterns of genetic diversity within a woody plant species (HAMRICK et al., 1992). The knowledge of the amount and distribution of genetic variation within a species is essential to the efficient design of sampling, genetic conservation, management, and breeding programs. This information could be

obtained from biochemical and molecular markers, morphological and physiological traits or from common garden experiments. Allozymes provide a good, quick method for estimating genetic variation, but the variation can be electrophoretically detected only for protein-coding genes and might not be adaptative in nature. In this study, we used both biochemical and morphometric data simultaneously. The study showed higher values of genetic diversity parameters in *R. auriculiforme*, as compared to *R. mangium*, as well as higher population differentiation (phenotypic variance) in *R. auriculiforme* in both isozyme and quantitative traits. This could be the result of relatively more variable topography and heterogeneous edapho-climatic habitats colonized by *R. auriculiforme* (BOLAND et al., 1990; KHASA et al., 1994a), which could promote isolation and habitat selection. Such positive correlation between genetic variation and environmental heterogeneity has already been reported by several authors (BOUSQUET et al., 1990; HAMRICK et al., 1991, 1992; LOVELESS, 1992). Low allozyme variation in populations of *R. mangium* could be accounted for by genetic bottlenecks and founder events that occurred during Pleistocene glaciations resulting in small refuge populations (MORAN et al., 1989b). This species, however, exhibited a great deal of provenance variation for quantitative and adaptative traits (KHASA et al., 1995c). This is similar to western redcedar (*Thuja plicata* DONN), which shows much more variation in quantitative traits and apparent lack of genetic variation as inferred by isozyme and terpene studies (G. NAMKOONG, pers. comm.), and different from *Pinus torreyana* PARRY ex CARR, which seems to have lost both variability in isozymes and quantitative traits through bottlenecks (LEDIG and CONKLE, 1983).

Although several studies of forest tree species have shown similar patterns of diversity in comparisons of allozyme and morphometric data (STUBER, 1990; HARTL et al., 1991; SCHAAL et al., 1991; see for review MITTON, 1994) or soil nutrients (XIE and KNOWLES, 1992), some have shown incongruence between different variability measures (RAJORA et al., 1991) or inconsistency among environments (GOVINDARAJU and DANCIK, 1986, 1987a,b). In this study, canonical correlation analysis appeared to be a better procedure to find gene loci and alleles potentially associated with quantitative traits and geographic variation. By using both biochemical and quantitative data, regression analyses also showed population differentiation associated with geographic origins. These findings are in agreement with those from WESTFALL and CONKLE (1992) and HAMANN et al. (1998) but somewhat different from MERKLE et al. (1988) who showed that multivariate techniques of allozyme variation patterns were not better than single-locus techniques for certifying seed or for designating breeding zones in coastal Douglas-fir.

Previous studies based on allozyme markers indicated considerable intra-population variation for both taxa, but with a substantial proportion of the total diversity residing among populations (MORAN, 1992; WICKNESWARI and NORWATI, 1993; KHASA et al., 1994b). Although much of the variation resided within populations, geographic differentiation among populations was more pronounced in quantitative traits than at the isozyme level for *R. mangium*. These earlier results were in agreement with those from ATIPANUMPAI (1989), who showed differences in morphophysiological characters among the natural populations of *R. mangium*, but with large variation among trees within each population. For *R. auriculiforme*, a good congruence in geographic variation patterns was obtained in both allozyme and quantitative traits. PINYOPUSARERK et al. (1991) also showed geographical variation patterns among *R. auriculiforme* populations rather than among families within populations based on morphometric markers. For both *R. auriculiforme* and *R. mangium*, provenance trials have generally shown that populations from the cluster PNG-QLD were superior in quantitative traits to those from the cluster NT-IND (KHASA et al., 1995c). Apparently, differences in the genomes between the two regions are so great that most characters, including isozymes, show distinct geographic separation (MORAN, 1992; KHASA et al., 1994b).

R. auriculiforme and *R. mangium* are closely related to each other and both species have been reported to hybridize artificially (SEDGLEY et al., 1992) and naturally in paratric and sympatric zones (SKELTON, 1987), but the extent and evolutionary significance of interspecific introgression have never been investigated. By calculating mean species centroids using PCA and CDA techniques among others (ADAMS, 1982; WHEELER and GURIES, 1987; BOUSQUET et al., 1990; WESTFALL and CONKLE, 1992), it is possible to detect and quantify possible introgressive hybridization among populations of both species when sampling is correctly done in allopatric, paratric, sympatric zones of species' distribution. For instance, the PCA was used to detect introgressive hybridization between *Alnus sinuata* and *A. crispa* using allozymes (BOUSQUET et al., 1990), and CDA was used to detect hybridization and introgression in white and yellow ladyslipper orchids (KLIER et al., 1991).

This study has shown that during domestication of *R. auriculiforme*, an initial low level isozyme assessment of the species is essential in defining efficient sampling strategies for seed collections and testing for growth performance. On the other hand, genetic diversity in allozymes of *R. mangium* is not related to quantitative traits and ecological factors. Therefore, preliminary surveys of electrophoretic variation should be complemented by studies of genecological variation and life-history variation. As shown in this study, the use of refined multivariate techniques is often the only mean of detecting meaningful relationships between molecular markers and quantitative traits variation. These techniques can also be used to detect introgressive hybridization and delineate boundaries of closely related species. Some authors have showed that selection of certain isozyme alleles were correlated with quantitative traits (STUBER, 1990; HAYWARD et al., 1994). Therefore, the use of genetic markers for the isolation of quantitive trait loci related to adaptative and commercial characters (LANDER and BOTSTEIN, 1989) now opens new horizons for better understanding the genetic architecture of quantitative traits, essential in genetic improvement and conserving biodiversity of various organisms including trees.

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